Title: Phenomena of subterranean life

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PREFACE.

This paper which has been written at somewhat short notice for a special object is rather an outline of work intended to be some day accomplished than a record of work already completed. In it an endeavour has been made to indicate the main problems that arise in connection with the subject chosen and as far as possible to give a statement of what has been already made clear by other researches. Some of the chapters have been written with some degree of fulness, others are only sketched in outline. The Crustacea have been treated throughout more fully as they have been more specially studied by the writer, and in the appendix a first contribution is made towards a better knowledge of the British Subterranean Amphipoda.

(The numbers given in brackets refer to the list of References given at the end of the paper.)

C O N T E N T S.

I. INTRODUCTORY.

The student of Natural History is constantly meeting with facts and phenomena that excite his wonder and admiration but perhaps there is nothing more striking than the manner in which living beings have pushed their way into every corner of the globe, and the variety of the means by which they have so adapted themselves to their surroundings that the continued existence of the species is secured even under what appear to be the most adverse circumstances. In the case of the human race the stern need to live has forced some to live in the frozen regions of the far North, others to spend their lives under a tropical sky either on arid deserts or in dense forests; some live far up on the mountain side exposed to the dangers of its snow and ice, while others brave the perils of the stormy deep and practically make their home on the water instead of on the land.

And/

And what is true of man is also true of the whole animal kingdom of which he forms a part. From the keenness of the struggle for existence Darwin might readily have deduced the conclusion that every spot on earth capable of supporting life at all would be occupied by its appropriate denizen and certainly this conclusion has been shown to be more and more literally true by abundant researches since his day. Thus to quote merely two examples:- Nansen in his "Farthest North" speaking of the animal and plant life that he found in almost every pool on the ice-floes says:-

"And these are small, one-celled lumps of viscous matter, teeming in thousands and millions, on nearly every single floe over the whole of this boundless sea, which we are apt to regard as the realm of death. Mother Nature has a remarkable power of producing life everywhere - even this ice is a fruitful soil for her" (1,vol. I. p. 332), and in his last little book, "The Science of Life", Mr. Arthur Thomson says:-

"The forms of life are so varied that there is almost/

almost no corner of the earth or sea where it would be safe to predict the absence of organisms. On the mountain top and the floor of the deep sea, on the polar snow and in the desert sand, in the Mammoth Cave and in the Great Salt Lake, almost everywhere we find life. It might, perhaps, be called a modern achievement, the demonstration of the almost universal distribution of organisms, and the recognition of the protean plasticity which enables organisms to adapt themselves to conditions which often seem to us most unpropitious." (2,p.91)

Living beings are found in the water, in the air, and on the land. In the ocean not only do they exist on the margin near the land in countless numbers and in infinite variety, but on the surface of the ocean far away from land are found many forms which if perhaps less numerous in species often make up for it in the incalculable number of individuals; while the deep waters of the ocean where no ray of light penetrates and no wave disturbs the everlasting stillness there are many animals that continue to exist notwithstanding the apparent/

apparent scarcity of food, the absence of light, and the enormous weight of the superincumbent water. The air is tenanted by an abundance of forms most of which it is true spend much of their lives on the land, but some of which can live for weeks hovering over the surface of the ocean and appear as little affected by fatigue as the waves beneath them. On the land we find living creatures everywhere; in dry deserts and in marshy wastes, high on mountain tops under ice and snow and in the deep waters of hot springs, in the running streams and in stagnant pools. Others again have found a home for themselves in the caves and underground waters of the earth and contrive to live there though the conditions seem about as unfavourable as those of the animals, similar to them in many respects, which dwell in the ocean depths.

It is of these inhabitants of caves and underground waters that we propose to give some account in this paper. They are now known to occur in greater or less numbers in many parts of the world, and though the forms found in different countries differ/

differ of course in many respects and in some cases have no doubt arisen independently still they present sufficient features in common to make it worth while studying them as a special group, while the conditions under which they exist are so abnormal and their environment apparently so simple that the study can hardly fail to throw some light on the phenomena of life in other places and under less peculiar conditions.

These animals have usually been spoken of as "subterranean" and though perhaps not quite perfect the term is a convenient one and may continue to be used. There are many other animals such as the mole, earth-worms and other burrowing creatures, which live in or under the ground and might therefore be in a sense called subterranean, but these are not included with the true subterranean fauna for they live near the surface of the earth and at times voluntarily come actually to the surface itself. They might perhaps better be looked upon as an offshoot of what Professor Dendy (3, pp. 99-119) has named the Cryptozoic Fauna i.e. those terrestrial animals/

animals "dwelling in darkness beneath stones, rotten logs, and the bark of trees, and in similar situations." Of course no fauna can be sharply defined from those that verge upon it and just as the Cryptozoic fauna passes gradually into the ordinary terrestrial fauna so through the burrowing fauna it passes on towards the subterranean fauna; still the latter is much better defined than many other faunal divisions; its members spend their whole existence in caves and underground waters well away from the earth's surface (though still at no great depth from it) and they never come to the surface except when brought there by accident. The forms that constitute this subterranean fauna though numerous enough are few in number compared with the terrestrial fauna and though no one naturalist could give an adequate account of the whole of them it will perhaps be possible to rapidly review some of their more striking characteristics and to dwell somewhat more fully upon the Crustacean members since these form ~~some of~~ one of the most characteristic and interesting divisions of/

of the fauna and have been more specially studied by the writer.

II. CAVES AND UNDERGROUND WATERS.

Before proceeding to consider the animals that constitute the Subterranean Fauna it will be well first to devote some little consideration to the situations in which they are found and the special conditions under which they live.

They are met with in caves and in the underground waters of many countries. In many cases instead of the phrase "underground waters" the word "wells" has been used, thus many authors have spoken of the various species of Niphargus, Crangonyx &c. as "well-shrimps"; so long as this is confined to popular language no great objection can perhaps be found with it but its use is apt to give rise to wrong impressions and to lead to the idea that the animals in question are confined to the wells or have risen in connection therewith. This of course is not the case for although the animals which live in the subterranean waters are in nearly all cases obtained from the wells they have no special/

special connection therewith beyond perhaps that they may be somewhat more numerous in the greater accumulation of water at that particular place; they have no doubt been in existence in their underground habitat long before the well was made by man and they are able to extend wherever the waters reach in sufficient quantity to give them means of making their way between the stones, soil, gravel &c. through which the underground stream flows.

Let us first see what is known with regard to the caves inhabited by a special fauna. To do this with any approach to fulness would require a volume in itself but a few illustrative facts may be briefly given. Perhaps the most famous cave of all in this connection is the Mammoth Cave of Kentucky, which together with others of the American Caves has been fully described by Hovey (4 ——) and, with special reference to its characteristic fauna, by A.S. Packard (5, p. 4.). This cave is the largest out of five hundred caverns estimated to exist in Edmonson County, Kentucky. These caves are excavated in the subcarboniferous limestone, and cover/

cover a more or less elevated area estimated to be 8000 square miles in extent. The subcarboniferous limestone in which these caves are formed is covered by a thin stratum mostly of sandstone pierced by thousands of sink-holes through which the surface drainage is carried down into the limestone fissures so that the drainage is almost entirely subterranean. (5. p. 4) It is important here to notice the abundant opportunities that are thus afforded by which surface animals can be carried down into the caves and, if they succeed in continuing their existence there, of thus forming an addition to the subterranean fauna, and I shall afterwards contrast this with the far fewer opportunities by which surface animals can be carried down into underground waters where these exist as they frequently do apart from caverns. In the Mammoth Cave the rate of erosion has been variable; "the older parts are perfectly dry and entirely free from stalagmitic deposits, indicating rapid erosion, followed by elevation, so as to deviate the water completely into other channels. In/

In the newer parts the water is still dripping from the surface above, and depositing stalactites and stalagmites." It is in the newer damper parts of the caves that the animal life mostly congregates. It is not necessary here to follow any further the general description of the Cave but a glance at the map prepared by C.H. Hovey and reproduced in Packard's Memoir will readily give a graphic idea of the immense size of the cave and of its great intricacy and of the abundant room that it affords in its many galleries and passages for separate colonies of subterranean forms.

The temperature of the Mammoth Cave has been carefully investigated by Hovey who found "that the highest degree reached at any time in any part of Mammoth Cave is 56° Fahr., and the lowest $52\frac{1}{2}$° Fahr.; the mean for summer being 54° and for winter 53°. The later is probably the temperature of the earth's crust in the region where this cave is located." These conclusions were confirmed by the readings of a thermometer placed in the Rotunda and observed almost daily for six months when it was found that during/

during the whole of this period it did not rise above 54° nor fall below 53° ; and they were still further confirmed by a series of observations made by Packard in August 1881 (5, p. 9). Animals that live in the Mammoth Cave have thus an environment which is characterised not only by absolute darkness but also by a very nearly constant temperature; there is practically no flora, the members of the fauna are few compared with those of the fauna of any similar area on the surface of the earth and they live in an atmosphere always calm, undisturbed by storms and unaffected by the changes of the seasons. It thus appears that we here have life under the simplest possible external conditions and that is why investigators have turned to the study of these cave animals in the hope of getting from them some clue that may be useful in helping to explain the phenomena presented by animals surrounded by a more complex environment. The animals found in the Mammoth Cave are enumerated by Packard on pages 9 and 10 of his Memoir and some of them will be specially referred to later on.

Another/

Another Cave that has been investigated by Packard and others is the Wyandotte Cave which "is situated 5 miles north-east of Leavenworth, the county seat of Crawford county, Indiana," and like the Mammoth Cave is excavated from a table-land of subcarboniferous limestone. Its passages are estimated to be 23 miles in extent, it is drier than the Mammoth Cave and its temperature is practically the same viz. 54°. Near it is situated the Little Wyandotte Cave and there are numerous other caves in Indiana all presenting more or less similar characters. The Nickajack Cave "is situated near that point of the southern boundary of Tennessee where it is joined by the line which separates the States of Georgia and Alabama" (5, p.18) and has been explored by the late Professor Cope (6), and its fauna described by him and Packard (7), who found that its aquatic cave life differed considerably from that of the Caves of Kentucky, Indiana or Virginia. This is of considerable importance from a theoretical point of view for it shows that these cave forms are descendants/

descendants of different out-of-door species from those of the caves to the northward and as they are nevertheless similarly modified in many respects they present phenomena that have a direct bearing on the question of "Convergent Evolution."

Other caves are found in Utah, in Colorado and in other parts of North America but the examples already given will be sufficient for our present purpose.

As regards the age of these caves and their fauna Packard and Cope came to the conclusion "that our true subterranean fauna probably does not date farther back than the beginning of the Quaternary, or Post-Pliocene period," and after further discussion of the subject Packard says:- "It seems, then, fair to assume that the final completion of the caverns, when they became ready for occupancy by their present fauna, may not date more than - to put it into concrete figures - from 7,000 to 10,000 years, the time generally held by geologists to be sufficient for the cutting of the present river gorge of the Niagara and the Falls of St. Anthony. We may, then, put/

put the age of our cave fauna as not much over from 5,000 to 10,000 years before the dawn of history, which itself extends back some 5,000 to 6,000 years." The age of the subterranean fauna is of special importance for where we know this with some degree of accuracy and know also (as we may in some cases) the surface forms from which the subterranean ones have arisen we have some hope of determining the rate at which development has taken place in these particular instances.

If we turn to the caves of Europe we find that though they are not of such magnitude as those of the American Continent they are yet numerous and widespread, while their fauna has been perhaps even more carefully studied. One great group of them which presents many features in common with the American caves is found in the Karst in Carniola on the flanks of the Julian Alps. This is a table-land of limestone so full of holes as to resemble a sponge, and all the rain that falls upon it is at once swallowed up and disappears in the underground channels, some of the holes that open upon the surface/

surface leading downward for several hundred feet. One of the best known of these caves is the famous grotto of Adelsberg near Trieste (8, p. 246-7). The fauna of these caves has been specially studied by Schiödte (9), by Joseph (10 and 11) and later on by Jurinac (12). Many other caves are to be found in other parts of Europe and have been investigated with regard to their peculiar fauna by numerous writers, thus Leydig has recorded the existence of Asellus cavaticus in the Falkenstein caves (13, p. 269) Parona has described blind crustacea from caves in Piedmont (14) while still more recently the Caves of Bosnia and Herzegovina have been explored by Apfelbeck (15) and those of the Jura district by Viré (16).

In England and Scotland I know of no special works on caves from the present point of view, but in Ireland the Enniskillen and Mitchelstown caves have been specially studied by Carpenter (17) Jamieson (18) and others, and their fauna as recorded by these writers presents several striking features, and some resemblances to that of some of the American/

American caves.

In Australasia there are many caves some of them, as for example, the Great Jenolan Caves of New South Wales, of great beauty and likely in the future to attract as many tourists as the Mammoth Cave now does but so far as I know no attempt has yet been made to ascertain if they possess a special fauna. The same remark may be made with regard to the caves found in various parts of New Zealand, though from one of them I have a specimen of a terrestrial Isopod (Philougria) which was blanched in colour but otherwise like a species commonly found throughout the country.

The caves that we have been describing have of course all been formed by the action of water and in parts of them underground streams still exist so that in these cases we may say that we have caves and underground waters combined, but in many places we have underground streams percolating through the sand and gravel of alluvial plains or through fissures and openings in other strata without any connection with caverns; and as I have already said I/

I am inclined to look upon the fauna of these underground waters as in some respects more purely subterranean than that of caves. In caves there are usually very numerous openings by which surface animals may be carried in, and as some parts are dry we may have in the caves both air breathing and aquatic forms and among these there are often many (sometimes spoken of as "twilight forms") which form members of a series connecting the cave forms with the surface forms of the surrounding district by very gradual transitions. In the pure underground waters on the other hand we can have only aquatic forms, the fauna is consequently much more restricted and the means of entrance are far less numerous than in the case of the caves so that as a general rule the fauna is more sharply marked off from the surface fauna than is that of the caves. Hence it is worth while devoting considerable attention to the existence and abundance of underground waters such as are now being spoken of. Though one is often apt to forget the fact a little consideration is sufficient to show that what we are accustomed to speak of as the solid/

solid earth is soaked through and through with water, often to a very considerable depth. Of the water that falls on its surface in the form of rain some is evaporated again into the atmosphere and some finds its way to the sea but a very large proportion sinks down into the porous strata of the country on which it falls and the wide distribution and frequent occurrence of springs and of artesian wells even in places where from the dryness of the surface one might least expect them show how far and wide these underground waters extend. Numerous examples have been given by Lyell (19, vol. I p. 385 &c.) to show that these waters extend to great depths and that various water-bearing strata may be met with, one below another, as in one case at St. Ouen, in France, where five distinct water-bearing beds were intersected in one well. The depth to which artesian wells have been sunk in many parts of France, Algiers and elsewhere also affords abundant evidence of the same thing and a fact incidentally mentioned by Wallace in his Malay Archipelago also points in the same direction. He says that in the little/

little island of Kilwaru situated in the straits between the islands of Ceram-laut and Kissa with water one-third mile wide on either side affording good anchorage there are wells of excellent drinking water although the island itself is not more than fifty yards across and does not rise more than three or four feet above the level of the highest tides - thus apparently showing that it must have deep-seated subterranean channels connecting it with other islands. (20, p. 375-6).

I have already described the underground waters of the Canterbury Plains in New Zealand in some detail in my paper on "The Subterranean Crustacea of New Zealand" (21, pp. 248-253) and it will be unnecessary here to describe them again, further than to say that in them are found abundant underground waters sometimes flowing as more or less distinct streams, at other times probably forming broader and less strictly defined sheets, and that although there is probably nowhere any large free accumulation of water it can percolate so freely through the loose alluvial deposits of which these plains are mostly/

mostly formed that there is abundant room for the numerous subterranean species which are found in them. In speaking of the forms obtained from wells in various parts of the world writers frequently speak of them as coming from "deep wells;" this has probably arisen partly from pure inadvertence and partly from a somewhat natural misconception. In some cases no doubt animal forms have been obtained from deep wells, thus Benedict has described three species of blind Crustacea from an artesian well in Texas 188 feet deep (22), and no doubt other similar examples might readily be brought forward, but as a general rule these underground forms and particularly the crustacea are obtained from wells that are supplied with ordinary suction pumps and therefore at the outside not much more than 30 feet deep. This certainly is the case with the blind crustacea obtained in Canterbury, New Zealand, where the waters in which they live are tapped over nearly the whole plain by suction pumps and the water thus obtained for domestic purposes. It is noteworthy too that in the deeper waters near Christchurch N.Z. which are/

are brought to the surface by means of artesian wells sunk to two different water-bearing strata, the first 70-100 feet from the surface and the second about 200 feet, no subterranean forms have been obtained though I have frequently looked for them in the water from the first stratum and others have sought for them in those of the second stratum and moreover since these waters are used for drinking and other purposes by a population of about 40,000 people it is hardly likely that the blind crustacea at anyrate would have been overlooked had they been present. Another system of artesian waters exists in Hawkes Bay in the North Island of New Zealand and has been described in considerable detail by Mr. H. Hill in several papers published in the Transactions of the New Zealand Institute (23 and 24) but here again no subterranean fauna has as yet been found. It is a matter of common knowledge that artesian wells have been sunk with great success in some of the parts of Queensland where water on the surface is very scarce and that from many of these an enormous flow of water has been/

been obtained proving to be of immense advantage to the settlers. Several reports on these artesian wells have been published by Mr. R. L. Jack, Government Geologist for Queensland, (25,26 and 27) and about two years ago I applied to him asking if any subterranean forms had been found in the waters of these wells. He replied that up to that time no such forms were known, and he promised to make further enquiries and investigations in that direction, though he pointed out that the force with which the water issued from the bores was in many cases so great that it would be quite impossible to try to collect the animals by means of a muslin bag over the mouth as can often be done in the case of suction pumps, for the bag would be instantly torn to shreds.

It would be interesting did time permit to follow Mr. Jack in his account of the geological conditions under which these artesians occur, in which he shows how the rain water sinks into permeable beds at their outcrops and thus gets underneath impermeable strata filling up the space into which/

which they flow more or less completely according as the inflow exceeds the outflow. He shows too that seldom are the beds arranged in the saucer-shaped plan like that for so many years figured in text-books to illustrate the arrangement of artesians in the London basin, but that the permeable water-bearing stratum usually exists between two impermeable layers that are either parallel or converging towards their lowest levels and that from the lower end there must be an outflow which in the case of most of the Austrälasian artesian systems can occur only below the sea level. The question of the submarine leakage of artesian waters has been dealt with also by Mr. A. Gibb Maitland, formerly of Queensland but now Geologist in Westralia who has considered artesian basins in countries other than Australian, the only part of his paper yet published dealing mainly with those of North America, and in it he shows that in most of these also there must be a permanent seaward flow outward from these artesian basins. (28). Mr. G. S. Griffiths in his Presidential address to Section E. of/

of the Christchurch Meeting of the Australasian Association has also written of the subterranean waters of Australia and has pointed out that along the great eastern Cordillera of Australia where the rainfall is greatest the superficial deposits, being composed of gravel and rock débris, are most pervious and that moreover the continuity of the strata of the plains is broken at the hill-foot; consequently a large proportion of the rain caught on the ranges leaks under the subsoil directly it falls and continues to flow on underground towards the sea, and as the water has never ceased to flow in at the upper end the deeper "leads" must be saturated with water right through from the mountain-foot to the Australian Bight where between Warnambool and the Murray Mouth, "the sea literally bubbles up with fresh water which has leaked up through the sea-sands." (29, pp. 235, 236.)

His description of the way in which the rain water soaks into the permeable strata mainly where these are broken at the hill-foot is interesting not only as showing the exact source of the under-ground/

ground waters but also as pointing out what is a probable means by which the subterranean forms gain entrance to these waters; for as I shall afterwards point out several of the underground Crustacea are most nearly represented on the surface by forms that now live in mountainous districts often at considerable elevations and it seems likely that the ancestors of the underground forms themselves once lived in similar situations and were carried into the earth with the inflow of the water in the way in which Mr. Griffiths describes. This has very possibly been the case with the blind Crustacea of the Canterbury Plains of New Zealand though as I have elsewhere pointed out there are probably ~~also~~ numerous other opportunities by which the animals may pass underground, for the rivers in their course over the plains are rapid and liable to frequent floods and often scour out new beds and expose fresh loose sand and gravel through which their waters could easily flow to join the subterranean streams, carrying with them perhaps some of the living forms that inhabit the beds/

beds of the rivers. (21,p. 250.)

The subterranean fauna of these Canterbury Plains like that of the Caves and underground waters of North America, must be very recent, geologically speaking. All the places where they have been found are marked on Professor Haast's Geological Map of Canterbury and Westland as either "post-pliocene alluvium" or "recent alluvium", most of them being in the latter (80). It will afterwards be shown that some of the forms are themselves ancient, but I am now speaking of the time at which they adopted a subterranean habitat, not of the age of the forms themselves.

Besides the forms occurring in caves and underground waters we occasionaly meet with others living in mines or other underground works constructed by man, and these are of special interest as transitional forms between the ordinary surface animals and the true subterranean fauna. As the age of the mines can of course be ascertained the length of time in which the observed differences from the surface forms have been developed can be therefore/

therefore also known. Schneider has carefully described a modified variety of <u>Asellus aquaticus</u> from mines at Freiberg, (56) and one of <u>Gammarus pulex</u> from Clausthal (5A) while Moniez has described a similar variety of Gammarus from Emmerin (57) and other forms that have likewise only recently taken to a life in caves are mentioned by Packard (5).

III. HISTORICAL SKETCH.

For an account of the growth of our knowledge on the subject of Subterranean Life reference may made to the Historical Sketch already given in my paper on the New Zealand Subterranean Crustacea, (21, pp. 165-180) for although this does not profess to deal with more than the Subterranean Isopoda and Amphipoda it will nevertheless be found to mention nearly all the more important works bearing on the whole subject. I shall here content myself with briefly mentioning some of the papers on the subject that have appeared since the date of the compilation of the Historical Sketch referred to.

A. S. Packard in 1894 published a further paper dealing with the origin of the Subterranean Fauna of North America (30) in which he gives a summary of some of the more recent papers on the subject and also those regarding "blind, non-cavernicolous or lucifugous forms", ~~the~~ observations on the condition of the eyes in the embryo or young of cave forms and/

and a discussion on the theoretical aspects of the facts thus brought forward. This paper along with that of the writer's on New Zealand Subterranean Crustacea was noticed by"W.G." in "Nature," July 4th 1895 (31).

Previous to the publication of Packard's paper further additions had been made to the known species of American Cave Animals by H. Garman who discussed the origin of the Cave Fauna of Kentucky and described some new insects (32,33,and 34), by S. Garman who described Cave Animals from South-Western Missouri, (35), and by Stejneger who has published a preliminary description of a new genus and species of blind Cave Salamander from North America (36). In his essay on the Fishes of San Diego **Eigenmann** briefly refers to and figures the embryo of Typhlogobius (37) one of the blind fish and he has quite recently written several other papers relating to various points with regard to the Subterranean Fauna but of these only brief abstracts have as yet been published, (38, 39 and 40), one of them entitled "A Case of Convergence" (41) is of considerable importance/

importance in connection with the theoretical bearing of the facts but unfortunately it does not deal with the point at issue with the fulness that one would desire.

Lönnberg has recently described a new blind species of Cambarus, viz. C. Acherontis, from Florida (42), other species of the same genus having been long known from the Mammoth and other caves, but the most interesting addition to the underground fauna of North America has been made by Benedict who has described a new blind species of Palaemonetes and one of Crangonyx and a new genus and species for a blind Isopod Cirolanides texensis all obtained from an artesian well 188 feet deep, the water being pure and of excellent quality with a temperature of 73° Fahr., (22). Unfortunately only brief preliminary descriptions of these forms have as yet been published but the Isopod is quite new to the subterranean fauna and is well worth further investigation while the Palaemonetes also has not hitherto been obtained from underground waters though a fresh water species is common in the rivers/

rivers of the United States.

Turning to Europe we find that Schmeil has added to the already known Fauna of the Adelsberg caves an oligochaete, a planarian, two species of Ostracoda and five species of Copepoda (43). The caves of Bosnia and Herzegovina have been fully investigated by Apfelbeck who has described from them many species the most interesting of which is perhaps a species of Cambarus (44 and 45) a species of the same genus (so richly represented in America), C. stygius, having been long before described by Joseph from the Carniolan Caves and described by him as being nearly allied to the American cave species Cambarus pellucidus. Lannelongue has recorded the presence of several insects and arachnida in the Dargilan Cave in the Département Lozère (46) and Carpenter has described several similar forms from the Mitchelstown cave in Ireland, (17). Among the cave crustacea considerably the most important work that has recently appeared is that by Vejdovsky on Crangonyx subterraneus Bate, (47) with which he unites the Boruta tenebrarum of/

of Wrześniowski (48, p. 677-687). He describes the external and internal anatomy of the animal in considerable detail, devotes much attention to the various sensory setae found on various of its appendages and makes reference to and comparisons with other previously described species of the genus. With regard to the minute anatomy of the eyes in cave specimens of Proteus anguinus and Talpa europaea, Kohl has a large and important paper (49) which is however known to me only through a notice of it by Lendenfeld (50).

Several interesting species have been described from caves in the Jura district by Viré (16 and 51). Dollfus (52 and 53) and Chrevreux (54) and will be spoken of in greater detail further on.

The only addition to our knowledge of subterranean forms of New Zealand has been the full description of a remarkable Turbellarian by Professor W. A. Haswell from specimens supplied to him some years ago by the writer from wells in the Canterbury Plains. (55).

IV. THE MEMBERS OF THE SUBTERRANEAN FAUNA.

It would be quite beyond the scope of the present essay even to enumerate here the various members of the Subterranean fauna and much more so to attempt any description of them. All that will be done therefore is to mention some of the most interesting and to describe a very few of these in somewhat fuller detail.

The subterranean vertebrata are very few in number, but several fishes are known from the caves of North America; these have been referred to the genera Amblyopsis, Chologaster and Typhlichthys.

Typhlichthys subterraneus was described in 1859 by Girard and is now known to be abundant in the subterranean waters east of the Mississippi and south of the Ohio. In 1889 Garman gave an account of a blind fish from some caves in Missouri (35) and referred it to Girard's species; recently however Eigenmann has studied it more carefully and compared it with specimens from the Mammoth Cave and finds that/

that the two are not only different species but are also of separate origin (41, p. 280); he has named the Missouri species Troglichthys rosae, and states that it (or similar species) has a wide distribution in the subterranean waters of the southern half of Missouri and northern Arkansas. In external form it very closely resembles Typhlichthys subterraneus but Eigenmann finds that it differs very much in the structure of the eyes which are much more rudimentary and present structures which, he says, show that it cannot have descended from the same form as the Typhlichthys subterraneus. In the meantime, however, his full account of the structure of the eyes has not yet been published. Two specimens of the Missouri species were studied by Kohl for his work already mentioned (49), but according to Eigenmann several of the structures were misinterpreted by him.

Among other vertebrata inhabiting caves may be mentioned the Proteus arguineus from Carniola and Dalmatia and the blind Salamander described by Stejneger from North America.

Turning/

Turning to the Invertebrates we find among the subterranean fauna great numbers of insects, especially Coleoptera and Thysanura, many Arachnida and Araneina and several Myriopoda. These being all air-breathing animals are found only in caves and though many of them present special points of interest they must be here passed over.

Among the Crustacea the largest and most conspicuous forms are the blind crayfish which are now known both from America and from Europe. The first American species was originally described by Tellkampf as Astacus pellucidus (58) and was afterwards placed in a new genus Orconectes by Cope (6) but Faxon in his "Revision of the Astacidae" (59) has assigned it to the genus Cambarus to which all the freshwater crayfish of the United States east of the Rocky Mountains belong, while Packard, after the manner of many American naturalists, retains the name Orconectes as a subgenus (5, p.42). In his larger work (5) Packard admits two species Cambarus pellucidus from the Kentucky caves and C. hamulatus from the Nickajack Cave and states that/

that it is obvious that the form from which the latter has been derived is quite different from that which has given origin to the former, and if this is really the case we appear to have here another example of convergence similar to that to which Eigenmann has drawn attention as stated above. The two species resemble one another in being blanched and colourless and blind. Cambarus pellucidus is considered by Faxon from the simple form of the male organs and the combination of characters belonging to different groups to be a very ancient form which has been preserved in the caves while its nearest kin have "succumbed in the sharper struggle incident to life outside, or were replaced by modified descendants"; (59, p. 42) this view is, he says, rendered more probable by the fact that it is found in the Wyandotte Cave on the other side of the Ohio as well as in the Mammoth Cave showing that "the subterranean waters of both localities derived this eyeless species from a similar form with well-developed eyes, that peopled the streams throughout this region at a remote/

remote period". W. P. Hay has published some observations on variations in the species <u>Cambarus pellucidus</u> and has described a new subspecies <u>C. pellucidus testii</u> (60) and as already stated Lönnberg has since described <u>C. acherontis</u> as a new blind species from Florida, (42). In Europe fresh-water crayfish have been found in caves by Joseph and Apfelbeck and it is very interesting to remember that these have been referred to the American genus <u>Cambarus</u> and not to the European genus <u>Astacus</u>, and though Joseph's description of his species is somewhat meagre and imperfect it is provisionally accepted by Faxon "as a witness to the former existence of the genus Cambarus in the rivers of Europe", and further on (59, p. 176) Faxon again makes use of the occurrence of <u>Cambarus</u> in the European caves in support of the assumption of the former coexistence of <u>Astacus</u> and <u>Cambarus</u> in the same area of distribution which he finds it necessary to make in order to explain the present, apparently anomalous, distribution of the freshwater crayfishes of the Northern Hemisphere.

The/

The only other stalk-eyed Crustacea known from caves are Troglocaris schmidtii Dormitzer, a fresh-water prawn from the Carniolan Caves, and Palaemonetes antrorum Benedict, already referred to as being obtained from an artesian well in Texas. So far as I am aware no similar animal is as yet recorded from any of the North American Caves, but in a collection of cave animals which I have recently received from Eigenmann there is what seems to be a species of Palaemonetes labelled as coming from the Mammoth Cave; it has, however, not yet been fully examined and I am unable to say whether it is a permanent inhabitant of the cave or not.

Vejdovsky who has published an elaborate account of the animals found in the underground waters near Prague (61) has described under the heading "incertae sedis" a very peculiar crustacean which he names Bathynella natans. Only two very small specimens were obtained from a well 20 metres deep and one of these was afterwards lost and his description is therefore somewhat meagre but from his figures the animal seems to be a Schizopod/

Schizopod without a carapace, and in this as well as in other respects it seems to come near the very remarkable Schizopod Anaspides originally described by G. M. Thomson from specimens caught in freshwater pools on the top of Mt. Wellington, Tasmania, at a height of 4000 feet, (62) and since then more fully worked out by Calman and by him considered to be a very ancient form showing distinct affinities with the fossil forms Palaeocaris, Gampsonyx and Acanthotelson; (63), if this is proved on further investigation it will be another example of an ancient form preserved in underground waters while its nearest allies on the surface have been replaced by other forms.

Of the subterranean Amphipoda by far the best known genus is Niphargus Schiödte, many species of which have now been recorded from various parts of Europe. It closely resembles the genus Gammarus, species of which are so common in freshwater and on the shores of all Europe but differs from that genus in having no eyes or at anyrate imperfect eyes, the terminal uropods with the outer branch very/

very long and two-jointed and the inner branch rudimentary, and the telson only deeply cleft and not actually double as in Gammarus. In England three species of Niphargus were long ago described by Spence Bate and Westwood (64) and it is rather strange that practically no further addition to our knowledge of the British Subterranean Amphipoda has yet been made; in the appendix to this paper I however make a start by giving a full and detailed description of Niphargus aquilex Schiödte which appears to be the commonest species in England. Niphargus has been recorded from Ireland but so far as I can ascertain it has never been taken in Scotland. Mr. Thomas Scott tells me that some time ago he made diligent search for it around Edinburgh without success. On the continent of Europe it is very widely spread and several species have been described by different authors, while other writers, especially De Rougemont, have considered all these are merely different forms of one species, the differences being supposed to be due to age and sex (65); the result has been much controversy/

controversy and little real advance of knowledge. Wrzésniowski has studied the genus with great care and has given by far the best account of the various species that has yet appeared (48) but it cannot be said that the question is yet permanently settled though it is quite clear that many of De Rougemont's assertions and conclusions were erroneous. Probably the fact really is that in the different isolated situations found in the underground waters local varieties arise and continue to breed true though in many cases they are hardly sufficiently differentiated to be considered as different species. Meanwhile new species continue to be described; Chrevreux not long ago described Niphargus Virei from the Jura caves (54) and he tells me by letter that he hopes soon to give a fuller account of this species along with descriptions of two other new species. Besides being found in underground waters one species has also been taken in the deep waters of some of the Swiss Lakes and has been described by Humbert under the name Niphargus puteanus var. Forelii (67) though it is now more commonly spoken of as/

as Niphargus Forelii. An interesting question arose as to whether this form was descended from some surface form in the lakes or whether it made its way into the deep waters of the lakes from subterranean waters around, in which it had previously existed. The question is fully discussed by Forel in his elaborate work "La Faune profonde des Lacs suisses" and though he had previously been of a different opinion he there comes to the conclusion that the Niphargus Forelii is directly descended from the N. puteanus of the subterranean waters (66, p. 179).

Another subterranean Amphipod closely allied to Niphargus is Crangonyx subterraneus, originally described by Spence Bate (64, p. 326.), the genus being new. Bate had only one specimen of his species and nothing further was recorded on the subject till Wrześniowski redescribed it as a new genus and species Boruta tenebrarum (48, p.677), Vejdovsky has however recently identified Wrześniowski's species with Spence Bate's and added a fuller description of it (47). A surface species Crangonyx/

Crangonyx recurvus has been found by Grube in Lake Vrana in the island of Cherso on the Illyrian coast and is mentioned by Heller (68) but I have not yet been able to get a description of it for the purpose of comparing it with the subterranean species. In North America numerous species of *Crangonyx* have been described some from the surface streams others from the underground waters; some of these however differ considerably from the European species and I am by no means sure that they are co-generic with it but it seems that the genus was once widely distributed for I have found in the subterranean waters of New Zealand a species which though quite distinct certainly comes under the same genus as the European *Crangonyx subterraneus* (21, p. 220). In the same waters there is also found a species of *Gammarus* showing that this closely allied genus was also at one time represented in the surface streams of New Zealand though it now appears to be found there only in the subterranean waters. *Niphargus* too is considered by most writers to be an ancient form and that it was probably/

probably once widely distributed is shown by the occurrence of two species, Niphargus montanus and N. mortoni in Tasmania. These species have been described by Thomson (69) and though they differ from the European Niphargi in the possession of eyes and in some other points they are certainly nearly related and appear to be another remnant of an ancient fauna preserved in this particular locality just as the Anaspides already mentioned has been.

The subterranean Isopoda are less numerous in species than the Amphipoda. In Europe only two species are known viz. Asellus cavaticus (see 70 p. 10) found in various caves and underground waters, and Asellus forelii described by Blanc from the deep waters of Lake Geneva (71); these belong to the same genus as the freshwater Isopod so common throughout Europe and do not appear to be so distinct from it as the subterranean species of Niphargus are from Gammarus. In North America several species of a similar kind are known though unfortunately these have been referred to a genus named/

named Caecidotea from a supposed but quite erroneous idea that it was closely related to Idotea; they are really near Asellus, a species of which, A. communis, is common in the United States. Much more interesting are the subterranean Isopods recently described by Dollfus from the Jura caves under the new genera Caecosphaeroma, Sphaeromides and Stenasellus (52 and 53). Here again owing to scarcity of material our knowledge is very limited but from Dollfus's figure of Stenasellus it is evident that it is a very interesting form differing markedly from Asellus in the cylindrical body and in the possession of a well developed pleon with four distinct segments. The genus Caecosphaeroma according to Dollfus belongs to the Sphaeromidae, and though he also refers his Sphaeromides to the same family it seems to me both from his figure and brief description to come nearer to the Cirolanides described by Benedict from the artesian well in Texas (22). All these Isopods are specially interesting because their nearest allies appear to be marine and with the possible exception of/

of <u>Stenasellus</u> no form at all nearly related to them is known from freshwater streams. That it would however be rash to assume therefore that they are directly derived from marine forms is clearly shown from the history of the genus <u>Phreatoicus</u>. This was originally described by the writer from a subterranean species found in New Zealand, (72). The genus was a very peculiar one combining characters of several of the families of Isopods and as no freshwater form at all resembling it was then known from any part of the world it seemed easy and natural to say that its nearest representatives appeared to be marine. A few years later, however, I received from the Australian Museum a small collection of crustacea and among these was a species of Phreatoicus that had been found in freshwater pools on the top of the Mt. Kosciusko Plateau in New South Wales at a height of 5700 feet. This species of course possessed eyes and differed in colour and some other respects from the New Zealand Subterranean species but it closely resembled it in all the generic characters that had/

had been laid down for Phreatoicus. It was fully described under the name Phreatoicus australis (73). Three or four years later another species was described by Mr. G. M. Thomson from the Great Lake, Tasmania, at an altitude of 3880 feet above sea level (74), and quite recently a closely allied form has been described by Baldwin Spencer under the name Phreatoicopsis from specimens found burrowing in the earth on the banks of the Upper Gellibrand River in the interior of Australia (75). It is thus abundantly evident that Phreatoicus is a very ancient form that has once been widely distributed in the freshwaters of the great masses of land in the Southern Hemisphere and is now preserved in these few widely separated localities while it has disappeared in the intermediate places through geographical and other changes. It differs from nearly all other Isopods in having the body laterally compressed and in the possession of a long pleon formed of six large and well developed segments; in these and some other characters it appears to approach the Amphipoda and has by some been looked upon/

upon as a form intermediate between the Amphipoda and the Isopoda and though I think this is erroneous and that it is an undoubted Isopod it is of such generalised character that I made for it a new family the <u>Phreatoicidae</u> (73) which appears to come nearest to the <u>Asellidae</u>. The Rev. T. R. R. Stebbing has thought it right to go a step further and in his "History of the Crustacea" has established it as a new Tribe, the <u>Phreatoicidea</u>, comparable to the whole of the <u>Asellota</u>. (76, p. 388). It is interesting to note that in the Asellid <u>Stenasellus</u> lately described by Dollfus the characters in which it differs from the ordinary Asellidae show affinity to the <u>Phreatoicidae</u> and that to some extent it seems to bridge over the gap between the two families.

Besides the Crustacea that have been already mentioned various Entomostracans have been described from subterranean waters and in greater abundance from caves. These include many Copepoda, and some Ostracoda and Cladocera. Cope has described a parasitic form Cauloxenus stygius found on a blind fish from a well near the Wyandotte Cave and the species has been also figured and described by Packard (5, p. 28). In his list of subterranean forms Moniez (57) includes several Protozoa, Rotifera, Gasteropoda and Turbellaria, and a similar list is included in Vejdovsky's account of the underground fauna from the neighbourhood of Prague, (61), but at the present time I shall mention only one or two remarkable "Worms" that have been obtained from the underground waters of the Canterbury Plains in New Zealand, chiefly through Mr. W. W. Smith of Ashburton. Perhaps the most remarkable of these is Phreodrilus subterraneus described as a new genus and species and made to constitute a new family of the Aquatic Oligochaeta by Beddard (77, p. 273). The genus is he says a very remarkable one, and, in addition to various/

various peculiarities in the internal anatomy the character of the setae is alone sufficient for the creation of a new family. Beddard regards the family as a very low form of Oligochaeta greatly specialised in certain directions. This case is interesting for it forms a parallel to the new family Phreatoicidae which had to be created for the Isopod already referred to and shows how rich the fauna of the underground waters of New Zealand is in peculiar forms. Another Oligochaete, Phreoryctes Smithii Beddard, has been obtained by me from others of the wells and in connection with this it is worthy of note that a species of the same genus, Phreoryctes Menkeanus, was many years ago described by Hoffmeister from specimens found in a well at Pyrmont and has since been taken in several other localities in Europe, (see Moniez, 57, p. 22). A remarkable Turbellarian has recently been described from wells in New Zealand by Haswell (55) under the name Prorhynchus putealis, but he only provisionally places the species under the genus Prorhynchus and says that the remarkable disposition of its reproductive/

reproductive organs "is one which is not paralleled, so far as I can ascertain, in any other Turbellarian, and is perhaps sufficient in itself, apart from the other points of difference, to render necessary the separation of the present form from Prorhynchus as at least generically distinct." (55 p. 642)

V. THE SPECIAL CHARACTERISTICS OF THE SUBTERRANEAN FAUNA.

We are now in a position to consider some of the most striking peculiarities presented by the members of the Subterranean Fauna as a whole and it will be convenient to do so under separate headings.

A. COLOUR.

All permanent residents of caves and underground waters are bleached and colourless. Packard who had the opportunity of observing cave animals belonging to many different classes says:- "we do not recall an exception to the general law, that all cave-animals are either colourless or nearly white, or, as in the case of Arachnida and insects, much paler than their out-of-door relatives (5,p.117.). This is certainly confirmed by the forms that I have myself examined which were uniformly pale and colourless, nearly translucent; the only exceptions, and these are trifling, are that in some specimens of the Amphipod Calliopius Subterraneus the yolk of the/

the eggs was of a light pink or rosy tint, the "liver"-tubes of Cruregens fontanus are pale yellow and the fluid in the vascular system of Phreodrilus Subterraneus is a fleshy red.

Similar evidence with regard to the colour has recently been given by Lönnberg (42) Carpenter (17) and Viré (16) and of the five species of Cyclops from the Magdalen Cave observed by Schmeil (43) all were colourless with the exception of Cyclops prasinus and he concludes therefore that individuals of this species living in places exposed to light must be very highly coloured.

The colour of subterranean animals is thus in somewhat striking contrast to that of the animals that inhabit the deep waters of the ocean for many of these are coloured, the crustacea particularly usually being of some shade of red or orange. S.J. Smith (78) considers that this shows that the darkness of the ocean depths must be very different from that of caverns and though this may be partly due to the phosphoresence of the animals themselves he does not think that it is wholly due to this cause. I have/

have suggested (21,p.260) that the difference in the chemical composition of the waters which form the environment in the two cases might have something to do with the observed difference in colour, and have endeavoured to test this by examining into the colour or want of colour of animals found in the deep waters of freshwater lakes but the facts that I have been so far able to gather do not lead to any very conclusive result.

Beddard has discussed the subject in his "Animal Coloration" and after rejecting the theory that the phosphorescence has anything to do with it says:- "The inevitable conclusion, therefore, from these facts appears to be that the brilliant and varied colorations of deep sea animals, is totally devoid of meaning." (79, p.37) It should be noted, too, that he says that "absence of light seems to have had no effect in the case of Manmalia which habitually live below the surface of the soil nor in earthworms or snakes which live underground. Uropeltid snakes, (Rhinophis oxyrhynchus), which live 'deep in the ground', and have degenerate eyes, are nevertheless/

nevertheless often marked with brilliant red and yellow colours. (79, p.64) It seems however quite probable that these members of the burrowing fauna are not so absolutely excluded from light as those of caves, and that the two cases are perhaps scarcely comparable.

LOSS OF EYES.

In all animals inhabiting subterranean regions the eyes appear to undergo more or less degeneration. Nearly all authors speak of the forms examined by them as having the eyes either absent or more or less imperfect. It is quite true as Schmeil has pointed out (43) that in some cases the eyes may be present and that there is merely a loss of pigment and again that in specimens preserved in alcohol the pigment of the eyes in some forms, e.g. *Cyclops*, may disappear and that mere superficial observations with preserved material are hardly sufficiently reliable in themselves to prove the actual absence of eyes, but even if we make allowance for these possible fallacies there are still left sufficient cases where the eyes have been carefully examined by sections and in other ways to prove/

prove the general truth of the statement already made.

Many contradictory statements have been made by different writers with regard to the presence or absence of eyes in subterranean animals; this is perhaps to be explained partly by the considerations mentioned above and partly by the fact that the various species actually do present differences as regards the eyes according as they have been a longer or a shorter time in their subterranean environment and again it is quite possible that we may have considerable differences in the condition of the eyes in the different individuals even of the same species. Thus Viré (51) remarks that in the animals examined by him the amount of degeneration is very different in different species and also in different individuals of one and the same species. In view of the varying statements that had been made by different authors on the eyes of <u>Niphargus puteanus</u> Leydig made special investigations on the species and found that the optic ganglion is present but not the eye though pigment spots mimicking the eye had led some observers to think that the eye was actually present. (81)/

(81). Schneider has described the commencement of degeneration in the <u>Gammarus</u> and <u>Asellus</u> examined by him from mines. (56 and 56a.) Packhard has investigated the condition of the eyes in many of the American Cave species and sums up the different results in the following words:-

"1. Total Atrophy of optic lobes and optic nerves, with or without the persistence in part of the pigment or retina and the crystalline lens. (<u>Caecidotea</u>, <u>Crangonyx</u>, <u>Chthonius</u>, <u>Adelops</u>, <u>Pseudotremia</u>.)

"2. Persistence of the optic lobes and optic nerves, but total atrophy of the rods and cones, retina (pigment), and facets (<u>Orconectes</u>).

"3. Total atrophy of the optic lobes, optic nerves, and all the optic elements, including rods and cones, retina (pigment), and facets (<u>Anophthalmus</u>, <u>Scoterpes</u>, and? <u>Anthrobia</u>)" (5,p.118).

He states too that we never find any rudiments of the optic lobes and optic nerves; if they are wanting at all they are totally abolished, while the external portions of the eyes (lenses etc.) may be found/

found in varying degrees of degeneration.

More recently the eyes in the blind crayfish of the American Caves have been studied by G.H. Parker (82) who summarises his conclusions as follows:- "In both species of crayfish studied, the optic ganglion and nerve are present, and the latter terminates in some way not discoverable in the hypodermis of the retinal region. In Cambarus setosus this region is represented only by undifferentiated hypodermis, composed of somewhat crowded cells, while in C. pellucidus it has the form of a lenticular thickening of the hypodermis, in which there exist multinuclear granulated bodies. These I have endeavoured to show are degenerated clusters of cone-cells."

The question of the structure of the eyes in underground species is of importance because some authors, notably Packard, have endeavoured to draw from the facts evidence of the direct inheritance of the effects of disuse, though others again deny that the facts point in this direction. The recent investigations by Kohl already referred to appear to have/

have an important bearing on the question but the subject is too large to be fully dealt with in the present essay.

C. COMPENSATION FOR LOSS OF EYESIGHT.

It has been stated by several authors that in subterranean species the loss of eyesight is more or less compensated for by increase of the other senses- touch and smell. Many of the species, especially among the Arthropoda, differ from their nearest surface allies in the greater slenderness of the body and greater length of some of the appendages. Thus in most of the species of Niphargus the body is much more slender than in the surface species of Gammarus and though the antennae and pereiopoda are not specially lengthened the terminal uropoda are very much longer than in Gammarus more especially in the male, and it is possible that this increase in length is associated with increased tactile powers. In Crangonyx there does not appear to be any such lengthening/

lengthening of the appendages except in C. antennatus in which Packard says the antennae are longer than in any other European or American species and in C. mucronatus in which the telson is unusually long. In the Isopod Caecidotea again the body is more slender than in the nearly allied form Asellus and the antennae and legs are longer. According to Packard (5, p. 123) the same thing is true of the cave species of Cambarus, and of some of the Myriopoda, Arachnida, and Insecta.

Among the New Zealand subterranean Crustacea we see some examples of the same thing - thus the blind species of Phreatoicus are distinctly more slender than the surface form P. australis found on the Kosciusko plateau and while there is no marked increase in the length of appendages in Crangonyx compactus, Cruregens fontanus and Calliopius subterraneus there certainly is in Gammarus fragilis for in this species both pairs of antennae, the last three pairs of pereiopoda and the terminal uropoda are all much longer than is usually the case in other species of the genus. It is curious to notice/

notice that while there certainly seems to be a tendency to increase in length in some of the appendages in the subterranean crustacea it affects sometimes one appendage and sometimes another. Thus in Crangonyx antennatus the antennae are unusually long, in Gammarus fragilis the last three pairs of pereiopoda and both branches of the terminal uropoda are increased in length, in Niphargus we find a similar increase in the outer branch of the terminal uropoda only, while in Crangonyx mucronatus these are of normal length but the telson is excessively developed and just as with the outer branch of the uropoda in Niphargus it is longer in the male than in the female.

In the case of the cave myriopods, arachnids, and insects it is very probable that the increase in length of the antennae and other appendages may be looked upon giving greater tactile powers and thus compensating for loss of eyesight and the same may be true also of the crustacea but I have elsewhere pointed out (21, p. 262) that the greater slenderness of the body in these forms (which are all/

all true underground forms and not specially connected with caves) may have been acquired to adapt the animal for its life in the restricted spaces between stones and gravel in which it has to live.

In some of the underground crustacea there are peculiar plumose setae which may perhaps be special organs of touch and in the case of _Cruregens fontanus_ and _Gammarus fragilis_ these appear to be more numerous than in allied surface forms but I cannot say that I have noted any special increase in their number in the other blind Crustacea that I have examined.

The "olfactory rods" that are found on the antennae of many crustacea are said by De Rougemont to be longer in _Niphargus puteanus_ and _Asellus cavaticus_ than in the corresponding surface species. This is confirmed by Fries, and by Leydig who also states that the same thing is true of the cave species of _Cambarus_. Professor Wright (American Naturalist, XVII p. 272) has stated that in these species the antennulary segments and olfactory organs/

organs are increased in number as well as in length; Faxon however finds that there is no increase in number though he agrees with other writers that the olfactory setae of Cambarus pellucidus are longer than in most species of Cambarus.

In the blind fish of the Mammoth Cave (Amblyopsis spelaeus) tactile papillae arranged in ridges on the sides and front of the head have been described by Tellkampf and others and by them considered to compensate for the want of sight. Similar ridges are found also in the other blind fish Typhlichthys subterraneus and what little is known of the habits of these fish seems to harmonise with the fact that they possess unusual powers of touch, hearing, and smell.

Other observations bearing on this point are given by Packard (5, pp. 123-130) and he quotes also similar facts from Joseph's paper.

D. ARRESTED DEVELOPMENT.

Several species of the underground fauna present/

present examples of arrest of development, that is they permanently retain characters that are usually found only in immature forms. Thus in _Cruregens fontanus_ from New Zealand the seventh segment of the pereion is small and bears no appendages, and in the Isopod _Caecosphaeroma Virei_ lately described by Dollfus from the caves of the Jura district the same character is present though as very few specimens of this species have as yet been found we cannot be quite certain that we are here dealing with adult forms. In the case of _Cruregens_ there is not the same doubt for I have examined scores of specimens and they all lack the seventh pair of pereiopoda and have the seventh segment of the pereion small. It is however worth while pointing out that in some Isopods the development of the seventh pair of pereiopoda is postponed to a comparatively late stage long after the animal has left the maternal pouch. I have elsewhere given several examples of this in the _Anthuridae_, the family to which _Cruregens_ belongs, and I have lately met a case of the same kind among the New Zealand _Oniscoidea_/

dea in the genus Scyphax which was established by Dana mainly on account of the absence of the last pair of pereiopoda. I find however that Dana's specimens were merely immature forms and that while specimens less than 5 mm. in length agree with his description, others a little larger (6 to 7 mm.)have the last segment of the pereion well-developed and the seventh pereiopoda present though they do not otherwise differ from the smaller forms which are equally active and present no immature characters beyond the one mentioned.

Similar cases of arrested development have been recorded in other cave forms by Heller, viz. in the glomerid Trachysphaera which has only 11 segments in place of 12 and 15 pairs of legs instead of 17, and in another Myriopod Brachydesmus which also lacks a segment. Packard has pointed out another example in the cave Myriopod Pseudotremia cavernarum which he says has only half as many segments as its out-of-door parent form Lysiopetalum.

Humbert has attributed this arrest of development in cave-animals to the influence of darkness, the/

the lack of sufficient food, and the other necessary conditions of their environment, (Archives des Sciences Phys. et nat. t. VII p. 266) but whether this explanation is adequate or not is perhaps doubtful.

VI. ORIGIN OF THE SUBTERRANEAN FAUNA.

While there has previously been considerable discussion on the subject and much diversity of opinion there can now be little doubt that the subterranean fauna found in any country has been derived either from the surface fauna that now exists in that country or from one that previously existed there. If attention had from the first been directed only to the air-breathing spiders, myriopods, insects &c., found in the caves there would probably never have been any doubt on the subject for they could only arise from a surface terrestrial fauna; but too great attention having been paid to the real or supposed affinity of some of the subterranean crustacea to marine forms has led to the mistaken idea that there was some connection/

connection between the subterranean fauna and the marine fauna. Thus Spence Bate has stated that the nearest ally of <u>Niphargus</u> is the marine <u>Eriopis</u> and that the marine <u>Gammarella</u> comes nearest to <u>Crangonyx</u> and the erroneous view first taken that <u>Caecidotea</u> was allied to the marine <u>Idotea</u> was supposed to point to the partially marine origin of the cave-fauna of America, and owing to imperfect knowledge of the facts a somewhat similar view was originally taken with regard to the New Zealand subterranean fauna. Fuller knowledge of the freshwater fauna of the different countries has already explained some of the cases that seemed to indicate a marine origin and further knowledge will probably clear up the following that still need explanation. Thus all the near allies of <u>Cruregens fontanus</u> at present known are certainly marine in habitat and I am not aware that any freshwater species of the <u>Anthuridae</u> has ever been described; the genera <u>Caecosphaeroma</u> and <u>Sphaeromides</u> in France and <u>Cirolanides in</u> America are also unrepresented in freshwater so far as our knowledge at present goes, but/

but the example of Phreatoicus which has been already related gives us good ground for hoping that evidence of their present or previous existence in freshwaters will hereafter be obtained.

Of the subterranean Crustacea in the Northern Hemisphere Cambarus, Palaemonetes and Asellus all have freshwater species from which the underground forms may have been derived and though the forms from which the underground Niphargus and Crangonyx have arisen are not so easily pointed out still it is clear that they belong to a group of Amphipoda that has long inhabited the freshwaters of the globe, and allied forms are still found in Europe (Crangonyx recurvus and C. pungens), Kamtschatka, (C. Ermanni) America (Crangonyx gracilis &c.) and even as far away as Tasmania (Niphargus Mortoni and N. montanus). Of the New Zealand subterranean forms two species belong to the genus Phreatoicus which I have already shown has probably once been a wide-spread freshwater species, one to Gammarus and one to Crangonyx both widely represented in freshwaters, another Calliopius subterraneus is very nearly allied to a freshwater form/

form Pherusa caerulea found on a mountain in New Zealand at a height of about 3000 feet, so that there is only left Cruregens fontanus for which at present no surface freshwater representative is known.

While the origin of the subterranean fauna from a surface fauna is therefore quite certain it is interesting to note that many of its members appear to be more ancient than the present surface fauna of the country in which they are found.. Thus Faxon considers that the cave species of Cambarus are ancient forms dating perhaps back to the time when Cambarus and Astacus were coexistent in the fresh-waters of the Northern Hemisphere; Niphargus is considered by Humbert and others to be an ancient form and not merely a modified descendant of the present freshwater Gammarus, and if we turn to the New Zealand species we find that in the present surface fauna of the Canterbury plains there are no near allies of the subterranean species; of these Phreatoicus by its generalised characters and former wide distribution and association in Tasmania with the still more generalised Schizopod Anaspides and with/

with other old forms is shown to be itself of ancient date, *Pherusa caerulea* the nearest ally of *Calliopius subterraneus* is known only from one situation 3000 feet above sea-level having apparently been superseded elsewhere by more recent forms, while *Gammarus fragilis*, *Crangonyx compactus*, and *Cruregens fontanus* have no known representative in the present surface fauna of New Zealand at all.

A full review of the subterranean species belonging to other groups would probably reveal other facts pointing in the same direction but these already given will be sufficient to show that by taking refuge in the recesses of caves and other underground places many ancient forms have been enabled to exist till the present day just as others have done (e.g. *Hatteria*) on isolated islands while they have become extinct elsewhere owing to keener competition in other more open situations.

VII. COMPARISON OF THE SUBTERRANEAN FAUNA WITH THE DEEP-SEA FAUNA AND WITH THAT OF THE DEEP WATER OF LAKES.

There are many points of resemblance between the animals found in the ocean's depths and those of the subterranean fauna while on the other hand there are some very striking differences and it would be interesting to make an extended comparison between the two and to compare both with the fauna of the deep waters of Freshwater Lakes as described by Forel (66.) and others, but this part of the subject has not yet been worked up and the heading is only given here to show that it has not been overlooked in the general scheme of the subject.

VIII. GENERAL CONSIDERATIONS.

As this is merely a preliminary report on the Phenomena of Subterranean Life it would be premature to attempt to discuss here the bearing that the facts have on the general biological theories and indeed to do so it would be necessary to range over the whole field of Biology for to fully explain even one species we must have complete knowledge of the whole. I shall merely indicate very briefly a few of the points that have been more specially discussed and leave them in the hope that they may be more fully treated when the present research is nearer completion.

Packard (5, p. 140) has drawn attention to the importance of Isolation as a factor in the origin of cave animals for by cutting them off from the possibility of interbreeding with the forms from which they have arisen their isolated life in the caves will have much to do with securing the stability of the new species. He claims that the cave fauna is almost completely isolated from that of the upper world; "indeed, far more so than the deep sea fauna of/

of the ocean or of lakes, or the faunas of deserts or of the polar regions, or the alpine inhabitants of lofty mountain summits", (5, p. 141) and as I have already endeavoured to show the fauna of underground waters unassociated with caves is probably still more isolated. The consideration of the influence of isolation upon cave animals leads one, he says, to attach greater weight than before to the importance of geographical isolation as a factor in preventing variation after the organisms have once been adapted to their peculiar environment. Darwin had long ago pointed out that if an isolated region be very small the total number of the species will be small, and this will retard the production of new species through natural selection by decreasing the chances of the appearance of favourable individual differences, and the truth of this is well shown by the case of the subterranean fauna.

The question of the polyphyletic origin of species naturally arises in connection with some of the underground forms. For example we have in Europe/

Europe many species of <u>Niphargus</u> differing only in comparatively minute points while resembling one another in other special characters, e.g. the size and structure of the terminal uropoda. It is hardly conceivable that one subterranean form arose in some locality and that all the others have arisen from this and even if this were possible in the case of the European species of <u>Niphargus</u> it could not be so with <u>Crangonyx</u> species of which are found in Europe, America and New Zealand. These must have separately arisen in these widely remote districts from a surface form existing there and the question is were the special characters of the genus already possessed by the surface form or have some of them been afterwards acquired independently in the different countries by the subterranean species as the result of similar environment. We know that the eyes + the colour have been independently lost in different forms from this reason - could the long and peculiar terminal uropods have been thus independently acquired?

Packard thinks that the two cave species of <u>Caecidotea</u>/

Caecidotea though alike in many respects have arisen from different species of Asellus and Eigenmann claims that he has in some of the cave fishes a clear case of Convergence. On the other hand Faxon speaking of the existence of Cambarus in caves in Europe as well as in America says:- "That the similarity of conditions affecting cavern life in all parts of the world is sufficient to bring about the close agreement between the crayfishes in Carniola and Kentucky, when the forms outside the caves belong to different genera in the two localities, seems highly improbable," (59 p. 42) and he explains the existence of Cambarus in European caves by the former existence of animals possessing the characters of that genus in the rivers of Europe.

The attempt to explain the loss of eyes in underground species has led to several theories and much fruitless controversy and the question can hardly be considered with reference to the subterranean forms alone for it raises the whole question of the inheritance or non-inheritance of acquired/

acquired characters and other considerations equally far reaching. Packard and others of the Neo-Lamarckian School in America explain it as due to the direct inherited effects of disuse, others by the results of the cessation of natural selection so far as the eyes are concerned since they are no longer of any use in the surrounding darkness, while still others speak of "economy of material," or point out that in the colonisation of the underground regions there is an active selection of the more perfect sighted since they naturally endeavour to make their way back to the light while others with less perfect sight love the dark places and making no attempt to get back to the surface sooner or later are carried underground and there give origin to the blind species; Darwin and others after him have suggested that in caverns eyes are not merely useless but, as delicate organs specially liable to injury, may be actually a source of danger to their possessors and would thus be eliminated by the action of Natural Selection just as winged insects have been on islands much exposed to wind.

The/

The question has been discussed at some length by Packard (5, pp. 137-143 and pp. 738-748) and by the writer (21, p. 266-271) while a summary of the more recent views on the subject is given by Lendenfeld (50, p. 14-19) but here the question must for the present be left for the attempt to discuss it further at the present stage of our knowledge would only lead to great waste of good ink and much mental confusion.

IX. APPENDIX ON THE
EXTERNAL ANATOMY OF NIPHARGUS AQUILEX SCHIÖDTE.

The species Niphargus aquilex which was described by Schiödte in 1855 appears to be the commonest subterranean Amphipod of the British Isles. Bate and Westwood (64, p. 318) record it from Maidenhead; Wandsworth, Surrey; and from Mannamead, near Plymouth; and they consider it identical with specimens found at various places on the Continent of Europe. Stebbing has recorded it from wells in the Isle of Wight and from Tunbridge Wells but though it is probably fairly common in many places I can find no further record of its occurrence in these islands though the same species or one very closely allied has been found in many places on the Continent.

Westwood who was the first to find the species in England identified it with Niphargus stygius Schiödte but on further consideration Bate and Westwood maintained it as a separate species under the name N. aquilex Schiödte, though not on the character "dorso carinato" that Schiödte originally relied/

relied for the separation of the two species. Wrześniowski considers it identical with the Gammarus puteanus Koch from Zweibrücken (not the form described from Regensburg described by Koch under the same name) and with Gammarus puteanus of Valette St. George and several other authors and from the examination I have so far made it appears very probable that this opinion is well founded. However the various species of Niphargus are separated by such minute characters and there is still so much confusion with regard to some of them that for the present I prefer to speak of this British species under the name that has usually been associated with it and to carefully examine it without at the time comparing it with the descriptions given of the continental species. When this has been done and the figures &c. then compared with those already given of the continental species or with actual specimens one will be enabled to arrive at a thoroughly independent and unbiassed opinion as to the question of identity or otherwise of the different species.

The/

The following description therefore and the figures given have been made from specimens from the Isle of Wight and Tunbridge Wells kindly supplied to me by the Rev. T. R. R. Stebbing and Professor D'Arcy W. Thompson of Dundee. At present I make no attempt to discuss the characters of the genus or of the other British species described by Bate and Westwood though material to enable me to do so at some future time is already in my possession.

NIPHARGUS AQUILEX SCHIÖDTE.

PLATES I and II.

Niphargus aquilex Schiödte, Comm. Soc. Reg. Dan. 1855, p. 350; Nat. Hist. Review. i, p. 41. fig. B.

" " Bate and Westwood, British Sessile-eyes Crustacea, Vol. i p. 315. [For other references and synonyms see Bate & Westwood l.c., Wrześniowski (48, p. 673) &c.]

The animal varies in size but full grown specimens are usually from 7 mm. to 10 mm. in length/

length of body. They are white and colourless and in the specimens that I have examined preserved in alcohol there is no external trace of eyes.

The body (fig. 1) is slender, considerably more so than in Gammarus, the head is longer than the first segment of the pereion, first four segments of the pereion subequal, the last three a little longer. The epimera of the first four segments are scarcely so deep as their respective segments, they are somewhat rhomboidal and directed a little forwards, most noticeably so in the first, their inferior margins rounded and supplied with a few small setae; the epimera of the last three segments more rounded below and not so deep. First segment of the pleon as long as the last segment of the pereion, second and third longer, subequal, the inferior margin of all three regularly convex, their postero-inferior angles rounded and bearing two or three small setae; fourth segment of pleon as long as the first, fifth and sixth much shorter.

The dorsal surface of the body bears a few scattered setae which are most noticeable on the last three/

three segments of the pleon.

Superior Antennae (figs. 2 and 3), as long as the head and first six segments of the pereion; first joint of peduncle as long as the second and third together and about $2\frac{1}{2}$ times as long as broad, a few setae on upper margin and at the distal end; second-joint rather more than half as broad as the first, three setae on upper margin and others at distal end; third joint half as long as the second and rather more than half as wide, a few setae at its distal end; flagellum about twice as long as the peduncle and composed of about 20 joints though the actual number varies slightly in different specimens; secondary appendage of two slender joints, the first twice as long as the second which reaches slightly beyond the end of the first joint of the flagellum and is tipped with three rather long setae.

Inferior Antennae (figs. 4 and 5) about half as long as the superior, peduncle longer than flagellum, the third joint short and broad, with a tuft of long setae at infero-distal angle, fourth segment with setae along upper and lower margins and a tuft of long/

long setae on lower margin at distal end, fifth joint about as long as the fourth, but narrower, similarly supplied with setae; flagellum composed of about 8 joints.

On both pairs of antennae are various sensory hairs or setae the exact number and arrangement of which I do not now propose to discuss; they have been very carefully examined in Niphargus Forelii by Humbert (67, p. 317-326).

The mouth parts present the usual characters found in the genus and I shall mention only a few special points: the mandible (figs. 6 and 7) has the palp large; its first joint slender, a little more than half as long as the second, free from setae; the second joint nearly half as broad as long, its outer border straight and without setae, inner border slightly convex and bearing about 10 setae of varying lengths; the third joint fully as long as the second, slightly curved, narrowed distally, its outer margin curved and free from setae, inner margin straighter and bearing on its distal half a close set row of short setae arranged regularly so as/

as to give it a comb-like appearance, at the end are three long setae and on the one lateral surface a tuft of three or four setae near the base, on the other two smaller tufts situated at about the proximal and distal ends of the middle third of the joint. In the right mandible the outer cutting edge is curved and formed of 5 or 6 teeth; the inner cutting edge is formed of 4 similar teeth of which the outer is the largest; in the left mandible the inner cutting edge is formed of one large tooth and a flat expansion serrated along its margin.

In the first maxillae (fig. 8) the palp bears 4 long setae at the distal end; the outer lobe obliquely truncate at the extremity and bearing about 10 strong setae most of which have one or more teeth on their inner margins, the innermost setae shortest and most dentate; the inner lobe very small and delicate and bearing on its inner border near the extremity a single seta.

The second maxillae (fig. 9.) have the two lobes subequal, rectangular, rounded at the extremity and each bearing there about a dozen long slender setae; the/

the outer lobe partially overlaps the inner and extends a little beyond it.

The maxillipedes (fig. 10) agree almost exactly with the description that Humbert gives for those of Niphargus Forelii but the row of setae on the lateral surface of the propodos contains only about 5 setae.

First gnathopoda (fig. 11) short and broad; the basos very broad distally though narrower at the base; posterior border with about 7 long setae distributed along its length, the more distal four being arranged in small dentations on the border, anterior surface with three long setae near the base and two near the distal end; ischium with a tuft of 4-5 setae on posterior border near the distal end; meros with its postero-inferior angle distinctly rounded and the distal portion of its free border supplied with about 10 setae of which one very long and strong one is situated about the middle of the border and four others in a regular row near the distal end; the carpus is about as long as the two preceding joints together and is concave below to receive the large propodos; its upper (anterior) border is slightly curved/

curved and has a transverse tuft of long setae near the distal end, its lower margin bears a regular row of about 6 long setae; the propodos is nearly quadrate though rather narrowed at the base and broadest distally where its breadth is slightly greater than its length; the anterior border regularly curved and bearing two transverse rows of setae one at the base of the dactylos the other more proximal; inferior border straighter and supplied with 5 short transverse rows of setae; the palm slightly convex, well defined by a stout spine-like seta near which are a few long slender setae and two stout pectinated ones; a few small setae are scattered on the lateral surface of the joint; the dactylos is stout, only slightly curved and fits accurately on to the palm.

The second gnathopoda (fig.12) closely resemble the first in shape and in the arrangement of the setae but are slightly larger; the basos is longer and slightly narrower and bears a greater number of serrations and setae on its posterior margin and in the propodos the posterior margin bears 8 transverse rows/

rows of setae.

The preceding description of the gnathopoda has been taken from a male specimen; in the female there will probably be found slight differences, but I have not yet had an opportunity of examining into this in detail.

The <u>first pair of pereiopoda</u> (Fig. 13) are rather slender; the basos is the longest joint and bears numerous long setae on both margins but especially on the posterior; the shape of the other joints and the setae thereon are of the usual character and will be readily seen from the figure.

The <u>second pair of pereiopoda</u> closely resembles the first.

The <u>third pair of pereipoda</u> (fig. 14) has the basos oblong with the postero-distal angle rounded, the anterior border bears 4 stout setae, the posterior bears several very minute setae; the other joints call for no special mention.

The <u>fourth</u> (fig.15) and <u>fifth</u> pairs of pereipoda closely resemble the third, but each is a little longer than the one preceding it. The propodos/

propodos appears to be somewhat loosely articulated to the carpus and may easily be made to revolve through a half circle, hence in fig. 15 it is drawn so that the dactylos points posteriorly though in its natural position it should be directed anteriorly as shown in figure 14.

The pleopoda are of the normal structure and present no peculiarities.

The first pair of uropoda (see figs. 16 and 17) have the basal joint rather longer than the rami, its upper surface flat or slightly concave each of its edges bearing 3 or 4 small setae; the outer ramus is a little longer than the inner and bears 4 small tufts of stout setae with a larger tuft at the end, the inner branch is similar but bears fewer setae.

The second pair of uropoda (figs. 16 and 17) reach as far as the end of the first and to the end of the base of the third pair, the base is as long as the rami and bears only two small setae on the upper margin at the distal end; the rami are equal in length and supplied with setae in a similar manner/

manner to those of the first uropods.

The <u>third pair of uropoda</u> (figs. 16 and 17) are greatly developed, especially in the male in which they are nearly as long as the whole pleon. The basal joint is stout, oblong, with one or two stout setae along its lower margin and several others at the distal end; the inner ramus is small, not so long as the base is broad, it bears 2 small setae at its apex. The outer branch is very long and is composed of two distinct joints. In the male the first joint is four times as long as the base, it is cylindrical slightly curved and bears 4 double tufts of short setae; the second joint is nearly as long as the first, but more slender; it is slightly curved towards the end, it bears no setae except three at the apex. In the female the first joint of the outer ramus is barely three times as long as the base and the last joint is only as long as the base; the arrangement of setae is practically the same as in the male.

The telson reaches as far as the end of the base of the third uropods, it is deeply cleft and each half/

half bears 3 or 4 stout setae at the end and one slender one about the middle of the outer margin.

DESCRIPTION OF PLATES I AND II.

All the figures refer to Niphargus aquilex Schiődte, figs. 1 to 16 are taken from a male specimen from the Isle of Wight, fig. 17 from a female specimen from Rusthall Common, near Tunbridge Wells.

Fig.	1.	Side view of male specimen, X 20.
"	2.	Superior antenna of the same, more highly magnified.
"	3.	Basal portion of the same, very highly magnified.
"	4.	Inferior antenna, highly magnified.
"	5.	The same - very highly magnified.
"	6.	Right mandible, showing palp; highly magnified.
"	7.	Extremity of cutting edge of the same, very highly magnified.

Fig. 8. First maxilla, highly magnified.

" 9. Second maxilla, highly magnified.

" 10. Maxillipede, highly magnified.

" 11. First gnathopod, highly magnified.

" 12. Second gnathopod, highly magnified.

" 13. First pereiopod, highly magnified.

" 14. Third pereiopod, highly magnified.

" 15. Fourth pereiopod, more highly magnified than fig. 14 (the propodos and dactylos are reversed).

" 16. End of pleon of male, showing uropoda &c., highly magnified.

" 17. End of pleon of female, showing uropoda, &c., more highly magnified than fig. 16.

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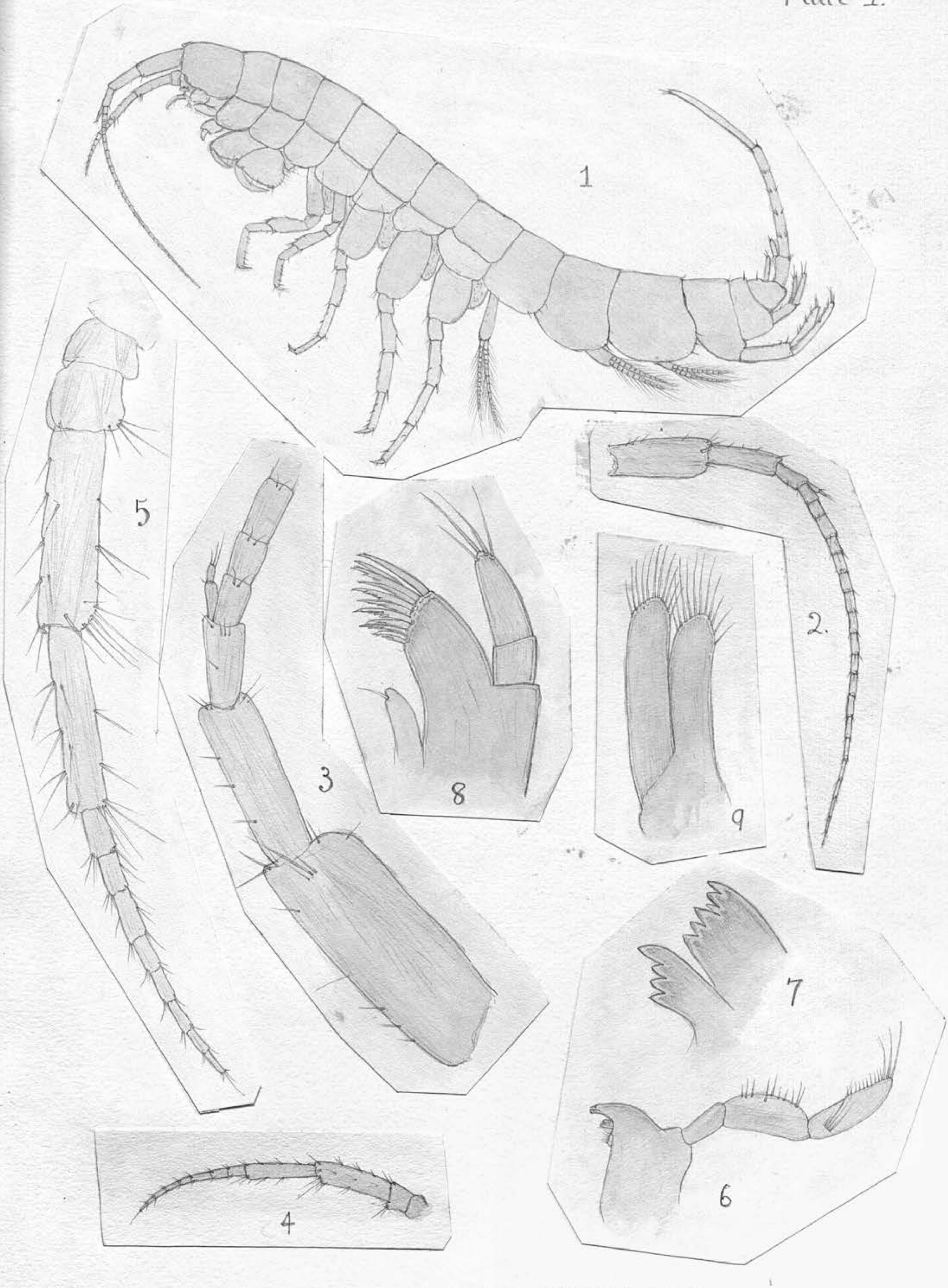
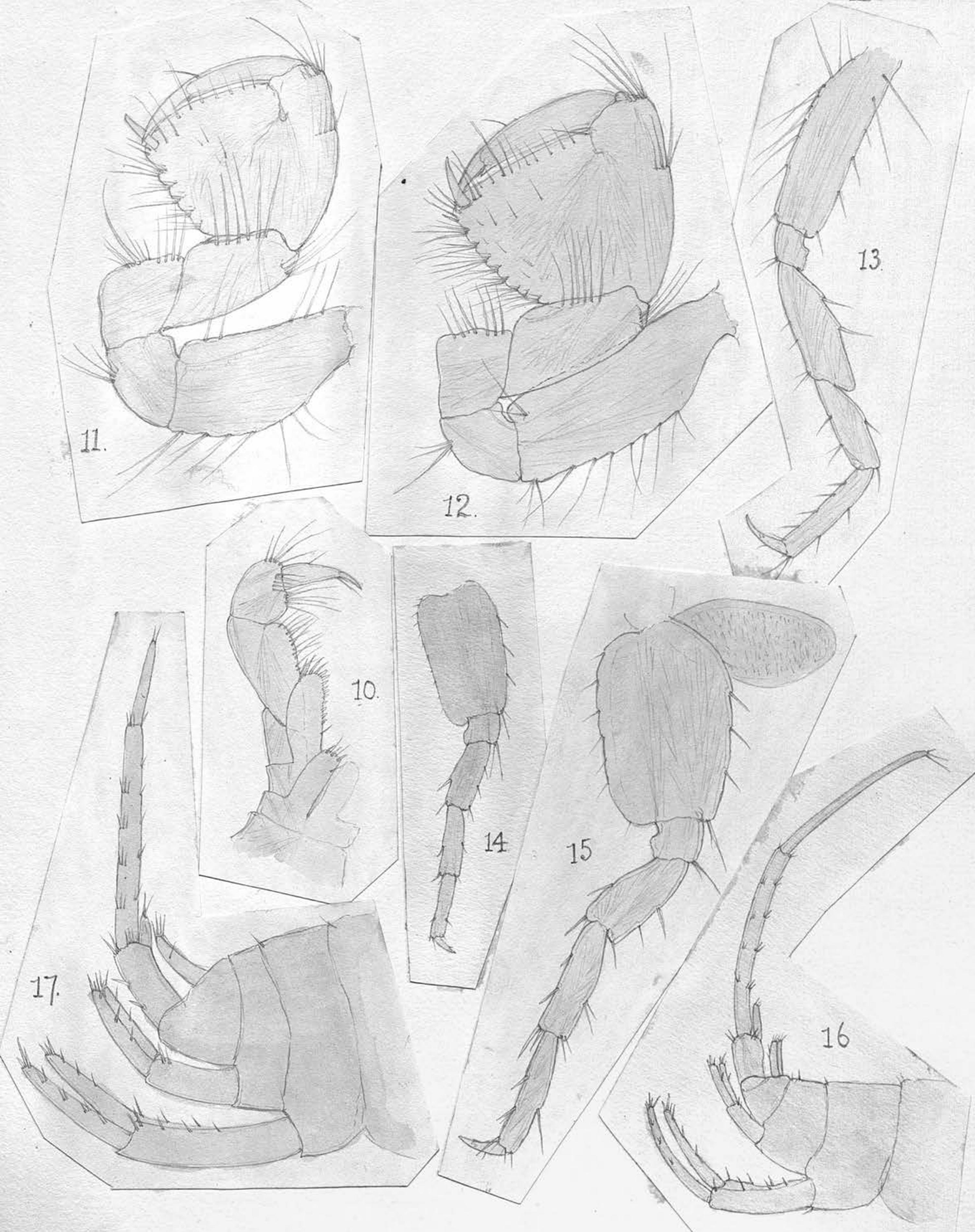
Plate I.



NIPHARGUS AQUILEX Schiödte.

Chas. Chilton ad nat. del.

Plate II.



Chas. Chilton ad nat. del.

NIPHARGUS AQUILEX, Schiödte.